that they are only modified in response to particularly salient events.

How might experience-dependent modifications at LOT synapses affect early olfactory learning? One attractive possibility is that a specific odor set, such as the odors associated with a mother, might cause a selective insertion of AMPA receptors at a small subset of LOT synapses when paired with a reward, such as a mother's milk (Figure 1B). These olfactory experiences may then set into motion a large-scale removal of NMDA receptors at LOT synapses but not at associational fiber synapses. The insertion of AMPA receptors at a limited set of synapses could account for the modest increase in AMPA receptor-mediated responses and could serve to increase the relative saliency of learned odors. The removal of NMDA receptors at LOT synapses could account for the large increase in the AMPA/NMDA ratio and might serve to limit subsequent NMDA receptor-mediated plasticity at these synapses. Coupled with plasticity in the olfactory bulb (Wilson and Sullivan, 1994), the aforementioned synaptic modifications could ensure that early olfactory experiences would strongly imprint a small odor set while limiting subsequent synaptic strengthenings associated with nonimprinted odors. Plasticity maintained at association fiber inputs, however, could still support olfactory learning throughout life (Haberly and Bower, 1989).

Although it is appealing to believe that early experience-dependent modifications across LOT synapses might increase the relative saliency of maternal and other learned odors, we must remember that there are simple, and no less important, alternative explanations for the synaptic changes observed at LOT inputs. For example, early odor experiences may serve to refine LOT inputs in a general manner rather than in a manner that increases the saliency for a small set of odors. Nevertheless, the findings by Franks and Isaacson further open the door to discovering the mechanisms whereby experience leaves its trace in olfactory cortex during early life. Many important questions stem from these findings. Do the observed LOT synaptic modifications contribute to early olfactory learning, or might they serve another purpose? What pattern of mitral cell activity initiates the downregulation of NMDA receptors at LOT synapses? What is the molecular signal that conveys the downregulation of NMDA receptors, and how is the pathway specificity of that signal achieved?

Future studies are needed to elucidate how or if the observed synaptic modifications in the olfactory cortex translate into olfactory learning and the encoding of memories, but an appealing hypothesis is that these modifications help establish strong olfactory memories in a small subset of LOT synapses. As a neuroscientist and a new parent, I cannot help but to wonder whether a synaptic trace is being left in my newborn daughter's olfactory cortex every time she breastfeeds.

Benjamin D. Philpot
Department of Cell and Molecular Physiology
Curriculum in Neurobiology
UNC Neuroscience Center
University of North Carolina
Chapel Hill, North Carolina 27599

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Resolving Border Disputes in Midlevel Vision

Two papers in this issue of *Neuron* specify the coding of border ownership, the basis of figure-ground segmentation, in early extrastriate visual cortex (area V2). Recording from a population of neurons, Qiu and von der Heydt show that border ownership assignments based on 2D images show the same bias when tested with stereopsis. Zhaoping shows that a neural model of V2 can make appropriate border assignments based on 2D images.

Everybody has seen Rubin's face vase demonstration, perhaps the most reproduced of all images from early 20th-century psychology. Yet even a century later, the fluctuation of figure and ground provide new insight into how we see and its possible neural basis. When our perception flips from the faces to the vase, the shape of the areas defined by the faces vanishes into the background and it appears to continue behind. In addition, when the vase is seen, the common border or contour between the face and vase "belongs" to the vase, whereas when the faces are seen, those common borders belong to the regions defined by the faces. This is a "border dispute" that continues unabated.

In less contrived scenes, this border dispute is more easily settled. Look at any of the three images (without stereoscopic fusion) that comprise Figure 1A. Even though the black region is consistent with the outlines of the letter C, it is seen more easily as a black letter O occluded in part by the small gray rectangle. The boundary between the occluder and the letter belongs to the occluder. It does not belong to black C-shaped fragment. This means that the black region at these contours is "unbounded." This allows it to complete or connect invisibly behind the occluder to other similarly unbound image regions to form the letter O (Nakayama et al., 1995). How this ownership is assigned is a chal-

lenging problem for human and computer vision alike. Sometimes called the segmentation/grouping problem, it is generally thought to involve midlevel processes, between the early coding of the image and object recognition.

Several Gestalt or contextual heuristics for 2D figures are relevant to segment this 2D scene. First, the rectangle is small, which usually indicates a figure, not a window or aperture. Second, four T junctions, where the edge of the small rectangle meets the black and white edge, are clues for occlusion.

Binocular stereopsis is also important. If two regions meet at a common border in a real scene, the closer region will always own the common border. Because binocular vision provides unambiguous information about depth, it provides the most decisive information about border ownership (Nakayama et al., 1989). The reader can fuse the left two or right two images of Figure 1A with either crossed or uncrossed eye alignments. When the gray patch is seen in front, it owns the common border that it shares with its black neighbor as before. As such, and even more strongly than in the 2D case, we see the black material continuing behind to form the letter O. Something altogether different and dramatic happens when the gray patch is seen in back. Rather than seeing the letter O, we unmistakably see the letter C. Why?

Because of stereopsis, the gray region is in back. Thus, ownership of the border is ceded to the black region. This region is thus delineated there by a bounding contour. As such, we see the letter C. By providing unambiguous depth information, stereospsis trumps other information in determining border ownership (Nakayama et al., 1989, 1995). So, both stereo and 2D image characteristics determine border ownership assignments.

These issues are further clarified in two important papers appearing in this issue of *Neuron*. These two papers link these processes to the very earliest stages of extrastriate visual cortical processing. Qiu and von der Heydt (2005) extend von der Heydt's lab's original discovery of cells that code border ownership in V2 and V4 (Zhou et al., 2000). In this earlier paper, they found that a significant proportion of cortical cells not only coded the well-known property of orientation, but also conveyed information about belongingness, which side owned the border.

Such coding is illustrated in Figure 1B, showing the localized receptive fields of the two border ownership neurons (BOWN) activated by edges. BOWN identity is depicted by the short arrow pointing to the region that owns the boundary. Thus, a cell coding that the boundary belonged to the gray rectangle is denoted by having arrows pointing inward with respect to this rectangle, whereas a cell coding a border that was owned by a surrounding region would be depicted by an arrow directed there.

Zhou et al. found for 2D images that, for a given receptive field, some cells would fire best if the edge of a small rectangle (figure) was on one side of receptive field, whereas some other cells preferred the small figure to be on the other side. Using stereo, they also found cells that changed their firing depending on whether the closer of two regions was on one side versus the other. These points can be illustrated diagrammatically in Figures 1B and 1C. As a convention, the receptive field of a border ownership cell firing the most at a given boundary is depicted in red. When defined by 2D Gestalt cues or when the gray patch is in front stereoscopically, border ownership cell firings would be as in Figure 1B. On the other hand, when the gray patch was coded in back because of binocular disparity, the firing patterns would be reversed (Figure 1C).

Interestingly, two cells were reported by Zhou et al. (2000) to colocalize these properties, so that for a small figure, the region of the figure defined by its small size coincided with that defined by binocular disparity. These anecdotal observations were tantalizing. It indicated that cells exist that code the customary relation between small convex image regions and objects in the real world, and it corresponds to our own perceptual biases. We see small enclosed image regions as figures, not as ground or windows or apertures. But two cells are too few to draw any conclusions. What was needed was a more systematic study of many cells to see whether this same joint coding persists for a large population of cells.

Qiu and von der Heydt (2005) recorded from 174 V2 cells. Each was tested to see if there were significant biases regarding border ownership. 35% were selective for the side of figure, 40% were selected for relative disparity (depth order), and 21% were selective to both. This latter class of cells was examined further, and 81% of these represented the "object" interpretation. This provides persuasive evidence that the association between these properties is not just by chance. It should be recognized that the bias is not expected to be 100%, as there are instances where surfaces do have apertures and where these relations between stereo and small enclosed 2D Gestalt figures would be reversed. Qiu and von der Heydt (2005) note that "…the influence of global configuration is still mysterious. Our results show that the range of this influence extends far beyond the limits of the classical receptive fields…".

It is to this issue of 2D global configuration that Zhaoping efforts to model V2 are directed (Zhaoping, 2005). The contribution is timely because she shows that by assuming a plausible set of inputs from area V1 and reasonable properties for a V2 network that the assignments of border ownership can be accomplished for large range 2D figures, which corresponds to our perception.

The V2 network has as its input V1 cells with oriented receptive fields. The specific connections and properties of putative V2 neurons are too numerous to detail here, but some embody plausible real-world constraints reminiscent of early computer vision models (Clowes, 1971; Huffman, 1977): excitatory connections between collinear border ownership neurons having the same sign; excitation of end-to-end units for those having the same sign and being part of a convex figure.

Other properties are those that realistically capture the biophysics and connectivity of cortex, such as the fall off of excitation and inhibition with distance. Most important is that this is a V2 model only; it does not entail back projections from other cortical areas. It is a recurrent network that uses border ownership neurons to adjust their outputs over time to arrive at a final bor-

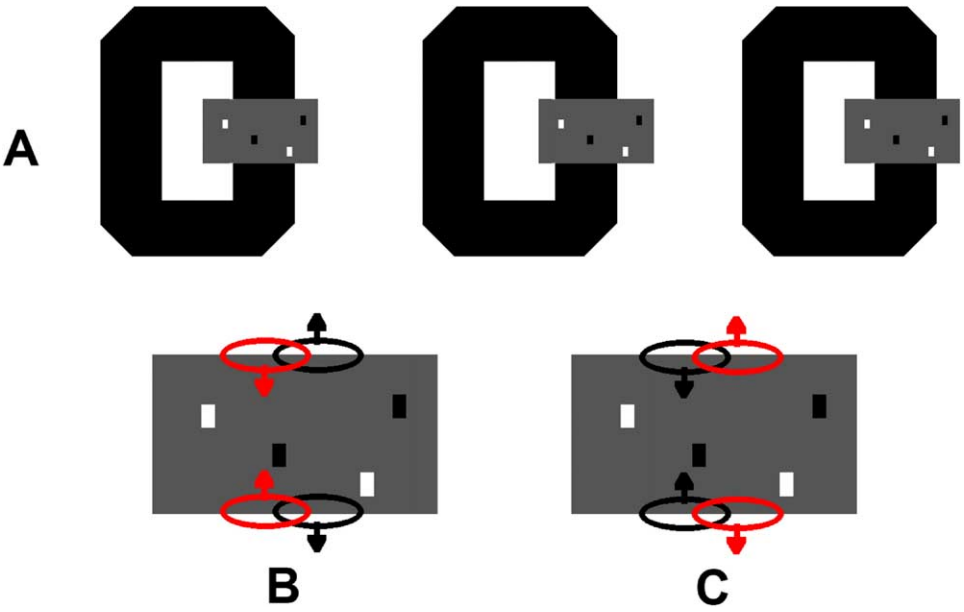

Figure 1. 2D and 3D Determinants of Border Ownership

(A) Stereogram allowing depth reversal by fusing either the leftmost or the rightmost image pair. When not viewed as a stereogram or when the gray patch is seen in front, border ownership coding in V2 is depicted as in (B). If depth is reversed, border ownership is depicted as in (C). See text.

der ownership signal throughout the network. One feature of the model (which distinguishes it from computer vision models) is that it does not rely explicitly on T junctions. These are difficult to detect in real images (McDermott, 2004), and their absence acknowledges this point.

The results are impressive. For a wide variety of complicated 2D situations with various figures that have been used in perceptual psychological experiments, the labeling is correct. This includes figures that are overlapping, some that have transparent junctions, and others that have invaginations that locally have concavities but are still part of a figure. So, as hinted by Qiu and von der Heydt's remarks, global 2D influence must go far beyond the confines of ordinary receptive field dimensions, and it is sufficient without top-down knowledge to do so.

Successful as each paper is at specifying interactions at the level of V2, the possibility of higher order feedback back to V2 cannot be excluded. The images used in all of these studies are much simpler and more easily segmented than those in natural scenes. Despite attempts to understand similar classifications in natural scenes (Geisler et al., 2001; Martin et al. 2004), it has been argued that stored high-level object knowledge is also required for segmentation (see Borenstein and Ullman, 2001). To this, several points deserve mention. Border ownership signals start within 10–25 ms after the initial responses in V2, suggesting that the processing must be fairly early and local (Zhou et al., 2000). Cortical conduction time over wide areas in V2 is fast, within reasonable ranges, except for fairly large stimuli, such that this should not pose a significant problem (Zhaoping, 2005). The existence of daVinci stereopsis, where unpaired points demarcate surface boundaries and border ownership suggests that surface processing must start very close to the output of V1. Eye of origin information is explicit only in V1 (Nakayama and Shimojo, 1990). With respect to high-level processes such as object recognition, border ownership dictates which letters are perceived, for example, the O or the C, the identity of the letters do not dictate border ownership relations (Nakayama et al., 1995).

With respect to how V2 might determine border ownership from 2D images, specific procedures to choose parameter values of the network are noted, "quantitative values for lateral connections are designed such that the desired contextual influence for BOWN are achieved….the model parameters are roughly robust once a desired parameter region is reached…" (Zhaoping, 2005). The task of setting of the parameters of the real V2 network does not have the wisdom and hindsight of modelers. This raises questions regarding system specification or learnability of network characteristics. Given that more local and assured information is available from stereopsis, could such signals help train networks to determine figure and ground in 2D images? Work in infant vision suggests that binocular depth perception develops before pictorial depth (Sen et al., 2001). Yet, that can't be the whole story, because individuals lacking stereopsis from birth are not lacking in pictorial perception, although it's conceivable that their pictorial development could be retarded.

These issues and speculations aside, the two papers in this issue highlight the fruitful confluence of psychology, neurophysiology, and computational modeling, a necessary interdisciplinary effort if we are to understand the circuitry of visual perception.

Ken Nakayama
Department of Psychology
33 Kirkland Street
Harvard University
Cambridge, Massachusetts 02138

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